A NEW TERTIARY FORMATION AND FAUNA FROM THE TIRARI DESERT, SOUTH AUSTRALIA

(A Contribution from the Museum of Paleontology, University of California, Berkeley)

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ABSTRACT

This report describes a new continental formation and vertebrate fauna from the east shore of Lake Ngapakaldi, a salt pan in the central Tirari Desert lying between the Birdsville stock route and the eastern shoreline of Lake Eyre in South Australia. The formation is a stream channel of friable, poorly sorted, pebble conglomerates, and shales cut into folded claystones of the mid-Tertiary Etadunna Formation.

The mammals are mostly woodland kinds, including koala-like, and ringtail and brushy-tail possum-like arboreal forms. A dasyurid, two bandicoots, a wombat, two rat kangaroos, a protemnodont macropodid, and a diprotodontid are also present. Most of the fossils are isolated teeth but there are several well preserved mandibles and numerous foot bones. Four isolated teeth questionably referred to the Monotremata are described. A new genus of wombat and a new genus of koala are proposed.

Other fossils include fish, chelonians, crocodile teeth, a lizard jaw and foot bones of a large emulike bird. Associated with the vertebrate fossils are impressions of *Eucalyptus* leaves and evidence of other plants.

The age of the formation and fossils is tentatively dated as Miocene.

INTRODUCTION

During the past ten years a sequence of middle to late Cainozoic formations and vertebrate faunas have been recognized by the South Australian Museum-University of California Expeditions in the Tirari Desert of the Lake Eyre region in South Australia. A preliminary report on this sequence was presented by Stirton, Tedford and Miller in 1961. The oldest unit is the rather widespread lacustrine Etadunna Formation (see Johns and Ludbrook, 1963) and its Ngapakaldi vertebrate fauna which was tentatively dated as late Oligocene. Following

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deposition, the Etadunna and underlying Mesozoic formations were moderately folded by an uplift that is thought to have occurred along an anticlinal axis roughly paralleled by the Marree-Birdsville stock route east of Lake Eyre.

Uplift along the eastern margin of the Lake Eyre basin modified the depositional regime within the basin with the result that stream channel and floodplain sands, silts and clays were superimposed on the folded Etadunna lacustrine deposits. The deposits of the new regime were recognized (Stirton, Tedford, and Miller, 1961) as three formational units, the Mampuwordu Sands, the Tirari Formation, and the Katipiri Sands which probably range in age from late Pliocene through late Pleistocene respectively. It was formerly thought that the relatively long period between the deposition of the Etadunna Formation and the Mampuwordu Sands was not represented by recognizable rock units or by fossil vertebrates in the Tirari Desert.

Evidence of an old stream-channel deposit that falls within this interval was discovered by Paul F. Lawson during the course of field exploration on the 1962 expedition. These deposits, herein described as the Wipajiri[4] Formation, were the subject of a preliminary description by us in 1964. The Wipajiri Formation contains a diverse vertebrate assemblage designated as the Kutjamarpu[5] fauna. Leaf impressions were found in the shales of the upper part of the Wipajiri Formation. Collection of the leaf impressions was hindered by the fact that the damp shales curled upon drying. They also were broken apart by the expansive action of salt crystals which formed on and between the laminae when exposed to the sun and air. We were able to secure a few impressions, however, and these, along with careful sketches (fig. 5) made at the outcrop in the field, have been studied by Dr. Harry D. MacGinitie, Research Associate of the Museum of Paleontology. Dr. MacGinitie has kindly permitted us to use the following statement, sent to the senior author in the form of a letter dated February 19, 1965:

"The leaf fossils brought to me by Mr. Michael Woodburne from the Australian locality no. V 6213 on the east shore of Lake Ngapakaldi are clearly the impressions of some species of *Eucalyptus*. Although there is not enough material on which to formally describe a new species, I can definitely say that the identification is without question.

"The impressions are those of lanceolate falcate leaves, width 2 cm., length 14 cm. (from the drawing made at the site); midrib slender; secondaries numerous, thin, flexuous, arising at angles of 45°, branching and anastomosing near the margin to form a characteristic marginal bend just within the margin; tertiary venation consisting of elongated meshes, the greatest length of the meshes parallel to the secondaries. The leaf is marked by numerous scattered, sclerophyllous dots which are usually seen in the leaves of the living species.

[4] *Wipajiri*. Tirari name for a site along the eastern side of Lake Ngapakaldi, meaning watercourse or stream; approved by the State Nomenclature Committee of South Australia.

[5] *Kutjamarpu*. New faunal name from the Tirari word meaning "many leaves"; approved by the State Nomenclature Committee of South Australia.

"Although it does not seem possible to distinguish the living species of *Eucalyptus* on the basis of their foliage alone, it may be profitable to call attention to the resemblance of the fossil impressions to the leaves of several species of lanceolate-leafed gums such as *E. marginata* Smith, *E. longifolia* Link, or *E. propinqua* Deane & Maiden."

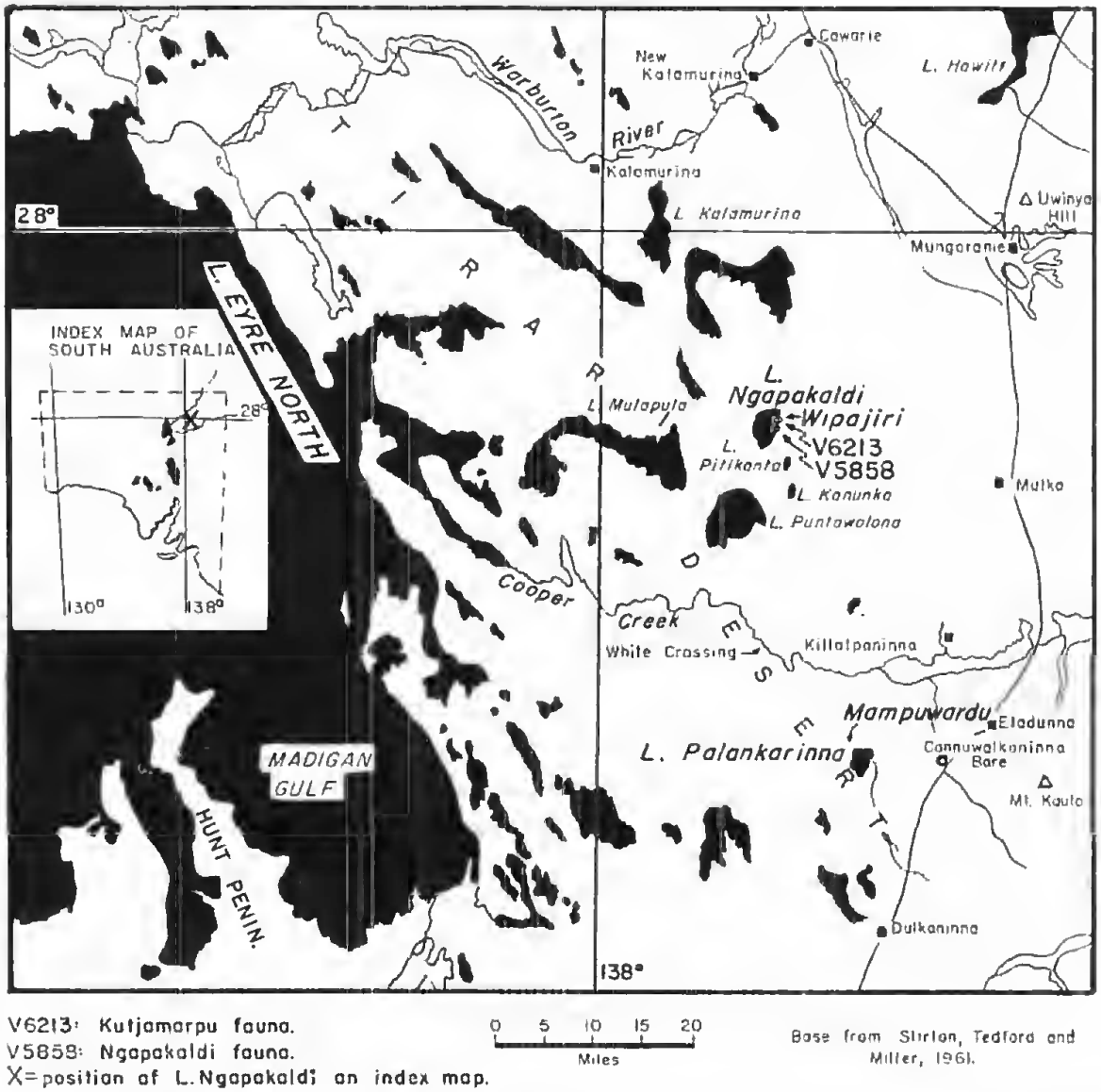

FIG. 1

Map of Tirari Desert, east of Lake Eyre, South Australia. Note position of Lakes Ngapakaldi, Puntawolona and Palankarinna.

Beginning about 1,200 feet north of Locality V5858 on the east shore of Lake Ngapakaldi (fig. 1), ferruginous conglomerates, sandstones and dark grey claystones crop out in an area about 50 feet wide and 900 feet long which follows the northeast trend of the shoreline of the lake (fig. 2). At the south end of the outcrop, the deposits are lost in the gypsiferous silts of the salt pan; to the north they are covered by Quaternary or Recent sand dunes. The Wipajiri Formation

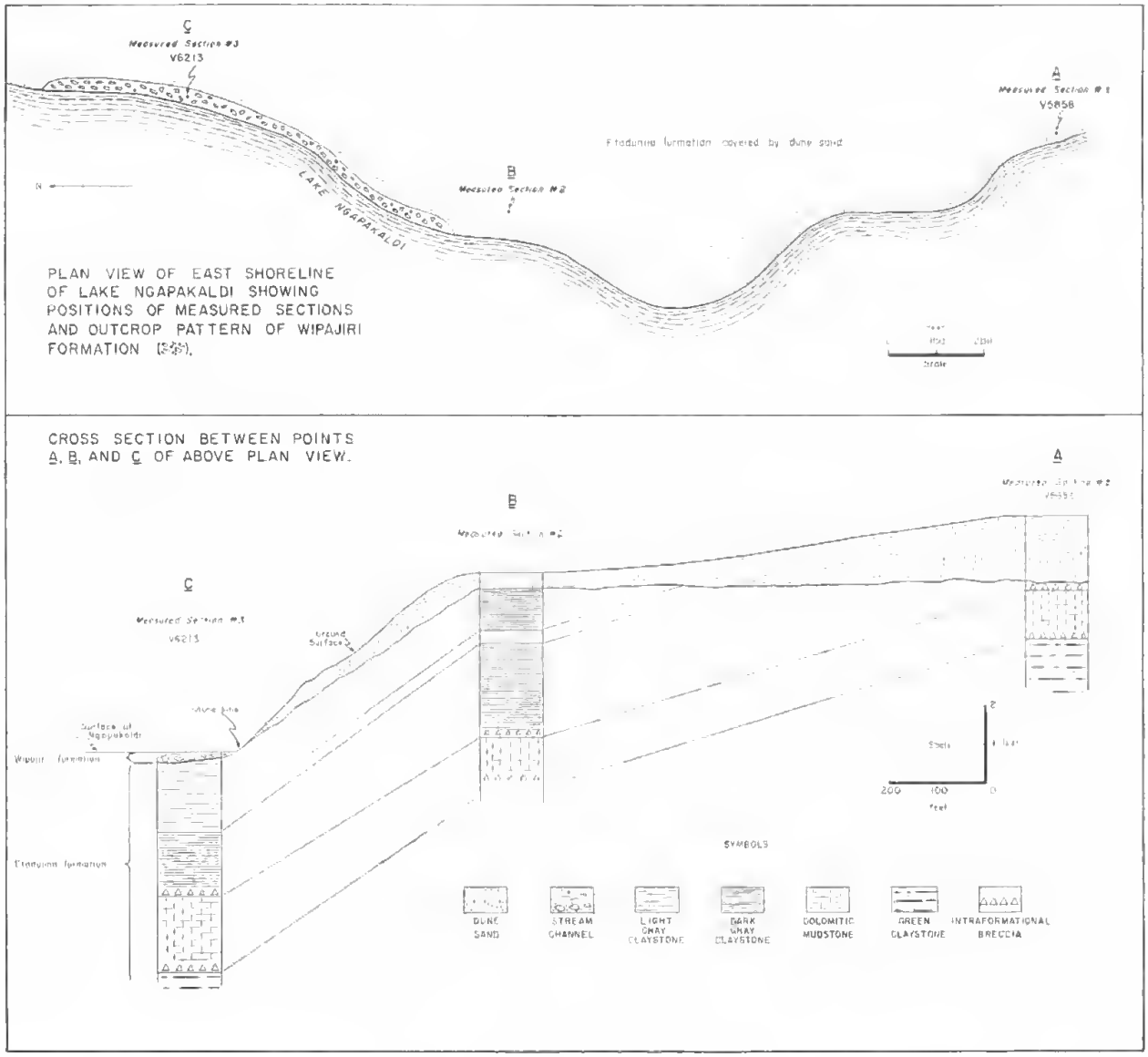

FIG. 2

(Above.) Plan view of east shore of Lake Ngapakaldi between fossil sites V-5858 and V-6213.

(Below.) Cross-section constructed between measured sections 1, 2 and 4 of the above plan view, showing northward dip of Etadunna Formation. Wipajiri Formation is channelled into the Etadunna at V-6213.

occurs in a north-easterly trending stream channel which is cut down into the claystones of the Etadunna Formation. Although the relations between the two formations appear disconformable, a slight angular unconformity is indicated by low angle tilting of the Etadunna Formation (strike N. 30°E., dip 2°NW). There is, however, no evidence for or against the Wipajiri being involved in the tilting, because of the limited extent of the exposure and the nature of the contact between the formations.

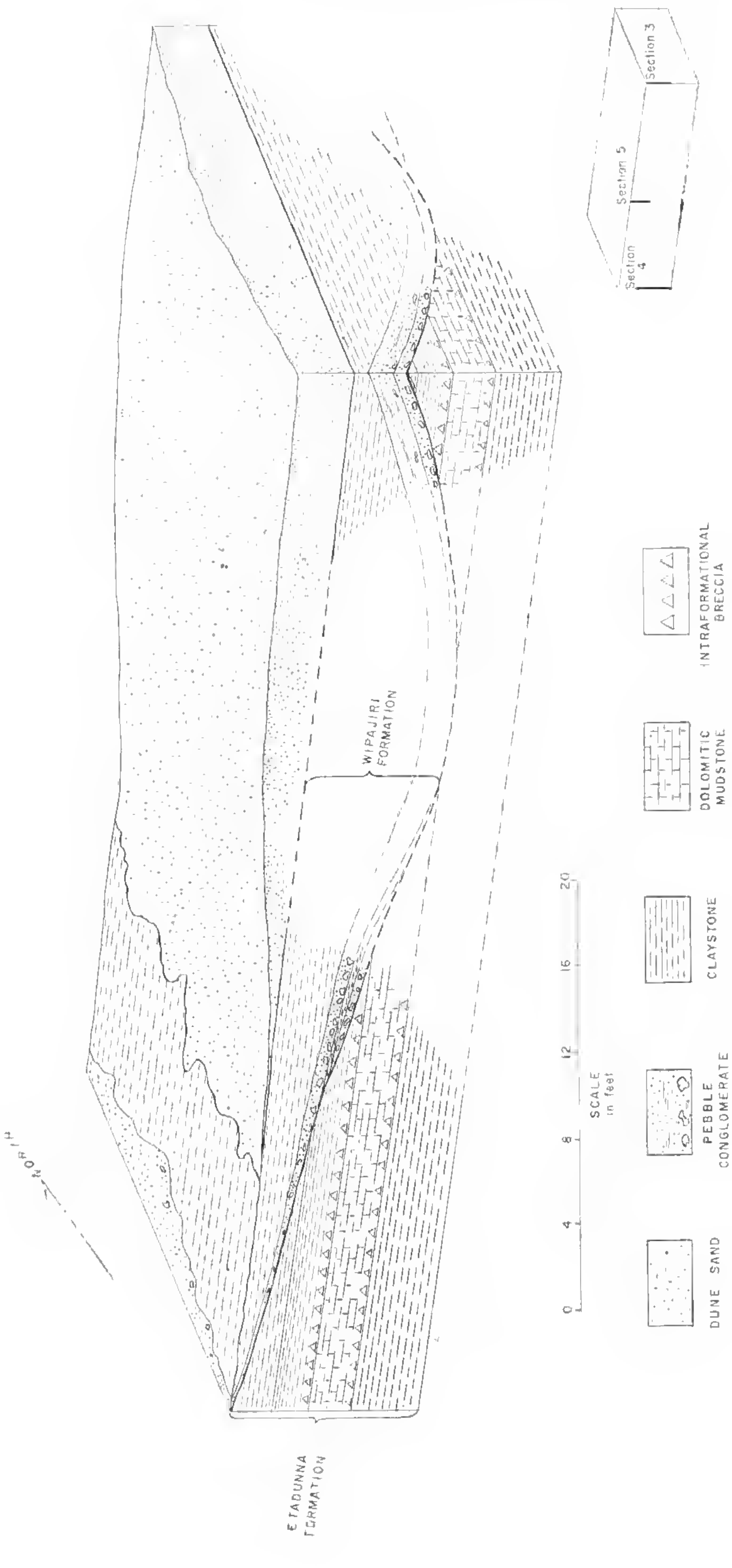

FIG. 3

Block diagram showing Wipajiri Formation channelled into the Etadunna. Small index drawing shows location of measured sections 3, 4 and 5 from which the block diagram was constructed.

The Wipajiri Formation can be subdivided into a basal coarse clastic portion overlain by finely laminated leaf-bearing shales (fig. 12, B). The coarse clastics (units 3 and 5 of measured section 5 in Appendix) contain the vertebrate remains, while the upper shales contain impressions of *Eucalyptus* leaves. The type locality of the formation is at UCMP Locality V6213 (fig. 12, A), 1,835 feet ... 1°E. of Locality V5858 (fig. 2). The outline of the main quarry at V6213 as well as the positions of other pits and measured sections is shown in fig. 4.

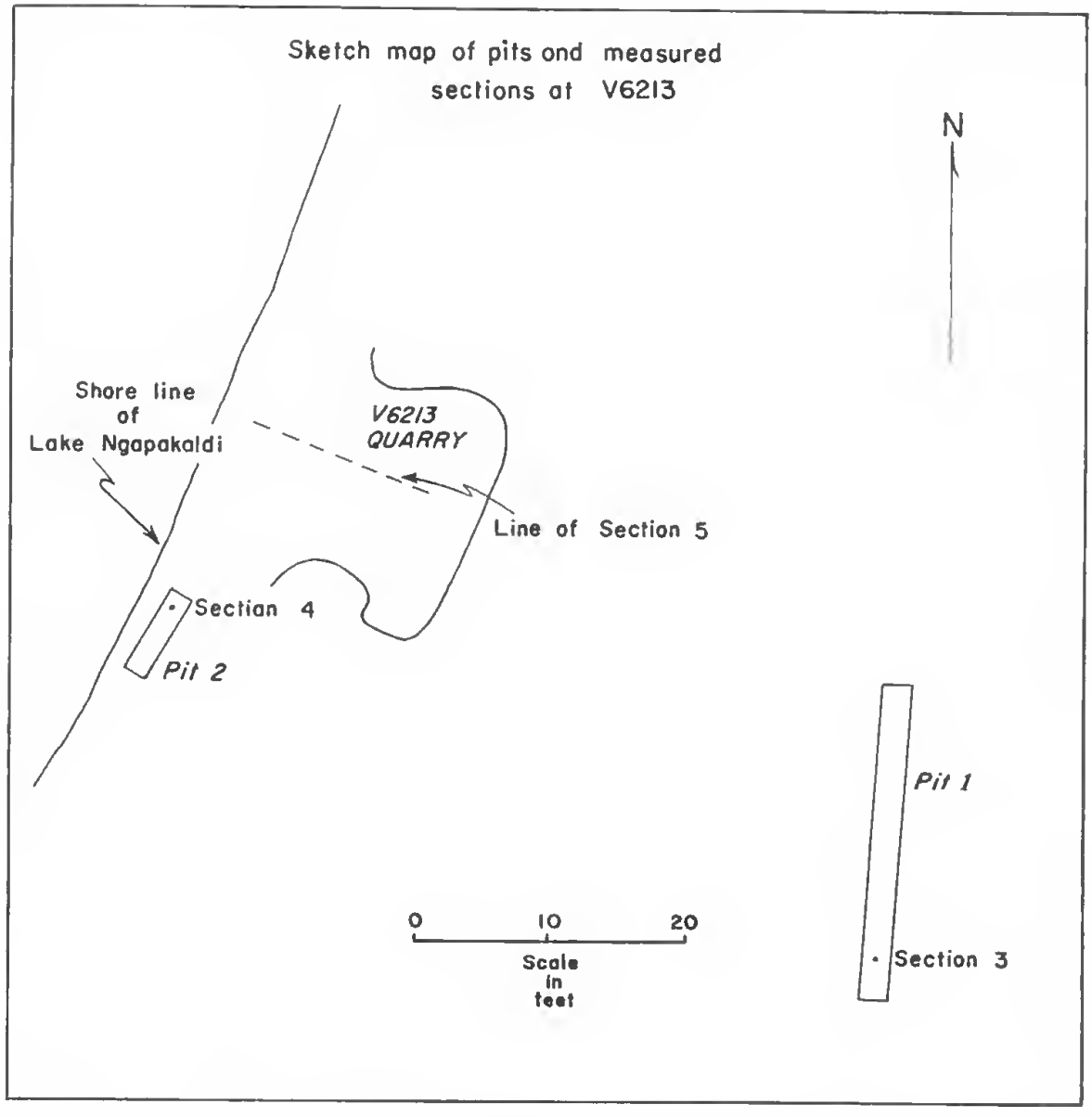

FIG. 4

Diagram showing location of pits, measured sections and outline of main quarry at V-6213.

The lower part of the Wipajiri Formation is composed of a basal conglomerate sequence (see measured section 5, Appendix A). The basal conglomerate is considerably coarser and more heterogeneous than the pebble conglomerate and apparently represents a more youthful stage of erosion with greater competence and velocity of the stream. The first two units are limited to the central part of the channel (see the block diagram, fig. 3) and are truncated by the pebble conglomerate. The latter unit contains the bulk of the Kutjamarpu fauna. The *Eucalyptus*-bearing shales of the upper, finely laminated portion of the formation have also yielded occasional turtle and fish remains in association with lenses of white sand.

Fortunately, the excavation represented by section 4 (fig. 4) is nearly perpendicular to that of section 5 so that the configuration of the channel may be readily seen (fig. 3). The trace of the deepest part of the channel trends about N. 26°E., which may explain the north-easterly trend of the outcrop pattern along the east shore of the lake. Figure 2 shows the northward element of the north-westerly dip of the Etadunna Formation between V5858 and V6213; fig. 2 and 3 show that the Wipajiri is channeled into the light grey and dark grey claystones of the Etadunna Formation. The dip of the Etadunna accounts for the fact that the Wipajiri Formation does not extend down to the fossiliferous green claystone of the Etadunna Formation, even though V6213 is topographically lower than V5858.

The Mampuwordu Sands at Lake Palakarinna represent a later phase of fluviatile deposition in the Tirari Desert. This deposit is composed of relatively clean white sands, light grey lenticular claystones, along with fragments of limestone derived from the Etadunna Formation and shows the following differences when compared with the Wipajiri Formation:

Mampuwordu Sands [Lake Palakarinna]	Wipajiri Formation [Lake Ngapakaldi]
1. Main clastic constituent is quartz sand, white to yellow, with only local centers of limonite stain.	1. Main clastic constituent is quartz sand, clear to amber, but more uniformly covered by limonite stain.
2. Clay occurs mainly as lenses.	2. Clay occurs in more persistent beds.
3. Derived clasts include durierust pebbles, Etadunna limestone fragments, milky quartz pebbles.	3. Derived clasts include durierust pebbles, irregular fragments of chert, ferruginous pebbles and cobbles, pre-Etadunna sandstone pebbles, Etadunna claystone, samlstone and calcareous mudstone pebbles and cobbles.
4. Crossbedding conspicuous and characteristic.	4. Crossbedding not evident.
5. Commonly a gypsum layer at basal contact.	5. No gypsum layer at basal contact.
6. On the whole, finer grained, cleaner, better sorted.	6. On the whole, coarser grained (in basal 1), more heterogeneous, less well sorted.

The "dirtier", generally coarser, more heterogeneous character of the Wipajiri Formation in contrast to the Mampuwordu Sands may be explained by a difference in source. The Wipajiri may also represent, at least in its initial deposits, a time of greater stream velocity and competence in a younger stage of erosion due to greater topographic elevation of the source area associated with regional uplift. "Regional uplift is reflected in the change from fine grained clastic and chemical sediments of the Etadunna to the coarser fluviatile deposits of the Mampuwordu Sands . . ." (Stirton, Tedford and Miller, 1961, p. 37). The contrast between the Etadunna and Wipajiri Formations affords the same inference. Also, the Etadunna is tilted at both Lakes Palankarinna and Ngapakaldi, although to a greater degree at the former. "At Lake Palankarinna the Etadunna Formation was folded into a broad syncline before the Mampuwordu Sands and horizontally bedded Tirari Formation were deposited. This folding may have corresponded with movements along the Mesozoic-early Tertiary anticlinal axis immediately to the southeast because the formations overlying the Etadunna are poorly sorted fluviatile deposits rich in fragments derived from a duricrusted terrain" (Stirton, Tedford and Miller, 1961, p. 32). Such an uplifted Mesozoic-early Tertiary anticlinal axis also may have served as the source for the Wipajiri Formation, in which case the terrain between the source and site of deposition (V6213) would have been of sufficient diversity to supply the duricrust and chert fragments, large hematitic clasts, pre-Etadunna sandstone clasts, and large Etadunna green claystone, sandstone and calcareous mudstone clasts found in the basal unit of the Wipajiri.

Nearly all of the larger clasts within the Wipajiri Formation can be traced to sources in the immediate area or regions farther east or southeast. The coarse clastic portion of this formation is made up to a large extent by round pebble to cobble sized clasts of green and grey sandstone and claystone, and white (usually mottled yellow by secondary limonite) calcareous mudstone derived from the immediately underlying Etadunna Formation. The bulk of these clasts are green sandstones and silty or clayey sandstones which do not crop out in the near vicinity and are relatively rare in the known outcrops of the Etadunna Formation. These probably represent basin margin facies of that formation which was being actively stripped when the Wipajiri was being laid down. Other argillaceous Etadunna clasts can be traced to sources at Lake Ngapakaldi or in the near vicinity.

The hard rock clasts include a variety of rocks most of which have been observed in outcrops in the anticlinal uplifts to the east. These include duricrust fragments and fragments of bleached sandstone. The polished grey duricrust pebbles, often three-sided, are types encountered in the Etadunna Formation, and may have been derived from that formation. The irregular chert clasts and large ferruginous fragments have not been observed in any of the previously described Cainozoic deposits in the Tirari Desert.

The abundant ferruginous clasts resemble laterites in that they are heavy, vesicular, iron-rich (31.0% Fe_2O_3) rocks. They have a granular texture, with grains about the size of a medium to fine sand. This reflects the texture of the parent sandstone because abundant quartz grains of similar size are preserved. These grains seem to be more completely replaced by limonite or hematite in the parts of the clasts which have the reddest colour. The largest ferruginous clasts observed were over 12 inches in maximum dimension, but the average would be only ten inches. Their size indicates that they were derived from a massive outcrop of ferruginous sandstone rather than one with a pisolitic structure. They cannot have been transported far as they are rather soft and yet have retained an irregular subrounded shape

The only local outcrop known to us in which similar iron-rich rocks are found occurs 10 miles to the south-west along the north-eastern shore of Lake Puntawolona. These deposits are ferruginous mottled fine grained quartz sandstones containing patches which are highly ferruginized. This outcrop seems to be a part of the irregular surface upon which the Etadunna Formation was deposited. Both Etadunna green claystones and fluviatile sands referred to the Katipiri Sands occur in the outcrop at Lake Puntawolona south of the ferruginized remnant, but their relation to the latter is obscured by drift sand. Other such remnants may occur in the vicinity of the Wipajiri type section, now buried under later deposits or exposed in salt pans not yet visited.

The irregular, subangular chert clasts range in size from less than an inch to several inches in longest dimension. They all have a conspicuously fibrous appearance which was at first mistaken for the texture of fossil wood. When broken, they are yellow brown, grey or blue-black and nearly completely replaced by silica, although they often show the remnant fibrous texture of their surfaces. These rocks have not been encountered in outcrop; they may be a primary silica deposit, as a siliceous spring deposit, or replacement of limestone. There is no resemblance to the known chert nodules in the Etadunna dolomitic limestone nor do these siliceous rocks show any trace of remnant calcareous material.

Most of the lithostratigraphic evidence merely indicates that the lower limit to the age of the Wipajiri Formation is post-Etadunna, as is that of the Mampuwordu Sands. Since outcrops of the Mampuwordu Sands occur some 35 miles south of those of the Wipajiri, the relative ages of these formations cannot be determined by physical stratigraphy. At Lake Palankarinna, the Mampuwordu Sands are overlain by the horizontal red argillaceous sandstones and arenaceous claystones of the Tirari Formation. These horizontal deposits also occur at Lake Ngapakaldi but, unfortunately, not in conjunction with the Wipajiri Formation. They are exposed near the top of the bluffs on the western side of Lake Ngapakaldi where they appear to directly overlie the Etadunna Formation (Stirton, Tedford and Miller, 1961, p. 57; note, the words "covered interval" should appear between units 3 and 4 of this section). The Wipajiri is covered only by Quaternary or Sub-Recent sand dunes so that its upper limit is not closely determinable by stratigraphic means. The geologic evidence indicates a post-Etadunna age for the Wipajiri Formation. Preliminary studies on the elements of the Kutjamarpu fauna corroborate this conclusion and further suggest that the Wipajiri is much older than the Mampuwordu Sands.

KUTJAMARPU FAUNA

The type locality of the Kutjamarpu fauna is UCMP Locality V6213, 1,835 feet N. 1° E. of UCMP Locality V5858 on the east shore of Lake Ngapakaldi, South Australia (fig. 1 and 2). The vertebrate fossils occur in the basal clastic portion of the Wipajiri Formation (units 3 and 5 of section 5; Appendix) where they are found as disarticulated skeletal elements. Spines of teleost fish are by far the most abundant, but mammal bones, jaws and teeth are common. The jumbled, disarticulated nature of the fossil remains is consistent with the stream-channel character of the deposit. In view of the relatively

high competence and velocity of the stream suggested by the size range and angularity of the clastic particles, the unabraded nature of the fossil remains indicates that they were derived from the immediately surrounding area rather than being brought in from far away. The

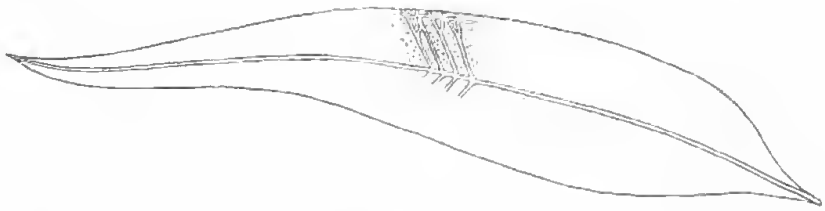

FIG. 5

Drawing of *Eucalyptus* leaf impression from the upper dark shale portion of the Wipajiri Formation at V-6213. One-half natural size.

leaf-bearing shales produced a few complete turtle carapaces and plastra and fish skeletons, and a partially complete lower leg and foot of an emu-like ground bird. These deposits contained the only associated skeletal elements.

The following preliminary faunal list will give an idea of the content of the Kutjamarpu fauna. Because of the preliminary nature of the present study, only a possible monotreme, a new wombat and a new koala will be described now. The diprotodontid, *Neohelos tirarensis*, has been described by one of us in another publication (Stirton, 1967b). The following Kutjamarpu vertebrates will be described at a later date:—Teleostei, parts of skeletons with bones in place, spines; Dipnoi, teeth; Chelonia, three carapaces, plastrons and foot bones; Squamata, mandible; Crocodilia, part of cranium, teeth, vertebrae, dermal scutes; Casuriiformes, part of pelvis, leg and foot bones; Dasyuridae, right mandible; Permelidae, upper and lower molars, and parts of mandibles; Phalangeridae (trichosurine and pseudocheirine), upper molars and mandibles; Potoroinae, maxilla, upper molars, mandibles, incisors, upper molars, lower molars, foot bones.

Class MAMMALIA

Subclass PROTOTHERIA

We have followed the practice of Simpson (1945, 1959, 1960) in retaining the Prototheria in the Class Mammalia. We agree, however, with the principle advocated by Huxley (1958) that any given category of classification should include the form, if known, which is ancestral

to the other taxa of that category. We thus believe that classifications should be formulated in the vertical, or clade, sense in so far as is possible.

Often, however, fossils are so poorly represented or preserved that the generic, familial or even infraordinal ancestor of a particular category cannot be determined. This is certainly true of the mammal-like groups of the Mesozoic. There is promise that the ancestral relationships of most of these groups will be clarified with future discoveries. Evidence from new discoveries, especially from the Rhaeto-Liassic, when adequate, supports the conclusion that most of the Mesozoic orders as well as the monotremes arose from different groups of mammal-like reptiles.

If the class Mammalia is to be restricted in scope we favour including therein the Theria and their Rhaeto-Liassic ancestors. In the meantime it is preferable to maintain the *status quo*.

Order ?Monotremata

Family *Ektopodontidae*, new family

Family diagnosis: That for genus until other genera or species are found.

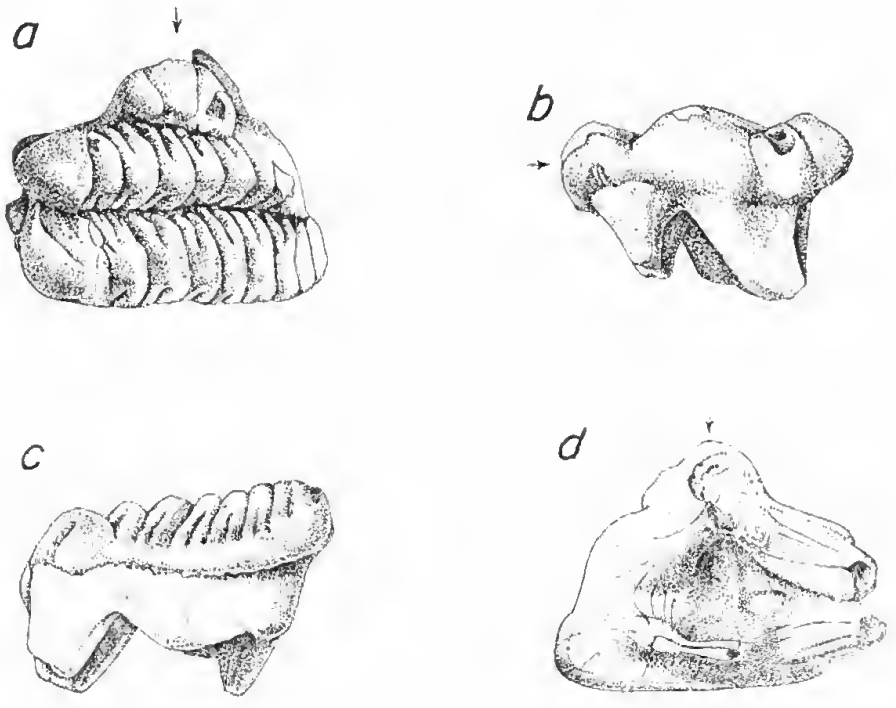

FIG. 6

Ektopodon serratus, n. gen. et. sp. Holotype. *a* occlusal, *b* labial, *c* posterior, *d* ventral views of SAM P13847, left upper molar. Four times natural size. Note appression facette at posterior base of crown. Arrow indicates anterior tip of tooth.

Ektopodon[6] Stirton, Tedford and Woodburne, new genus

(Figs. 6, 7)

Genotypic species: *Ektopodon serratus* Stirton, Tedford and Woodburne, n. sp.

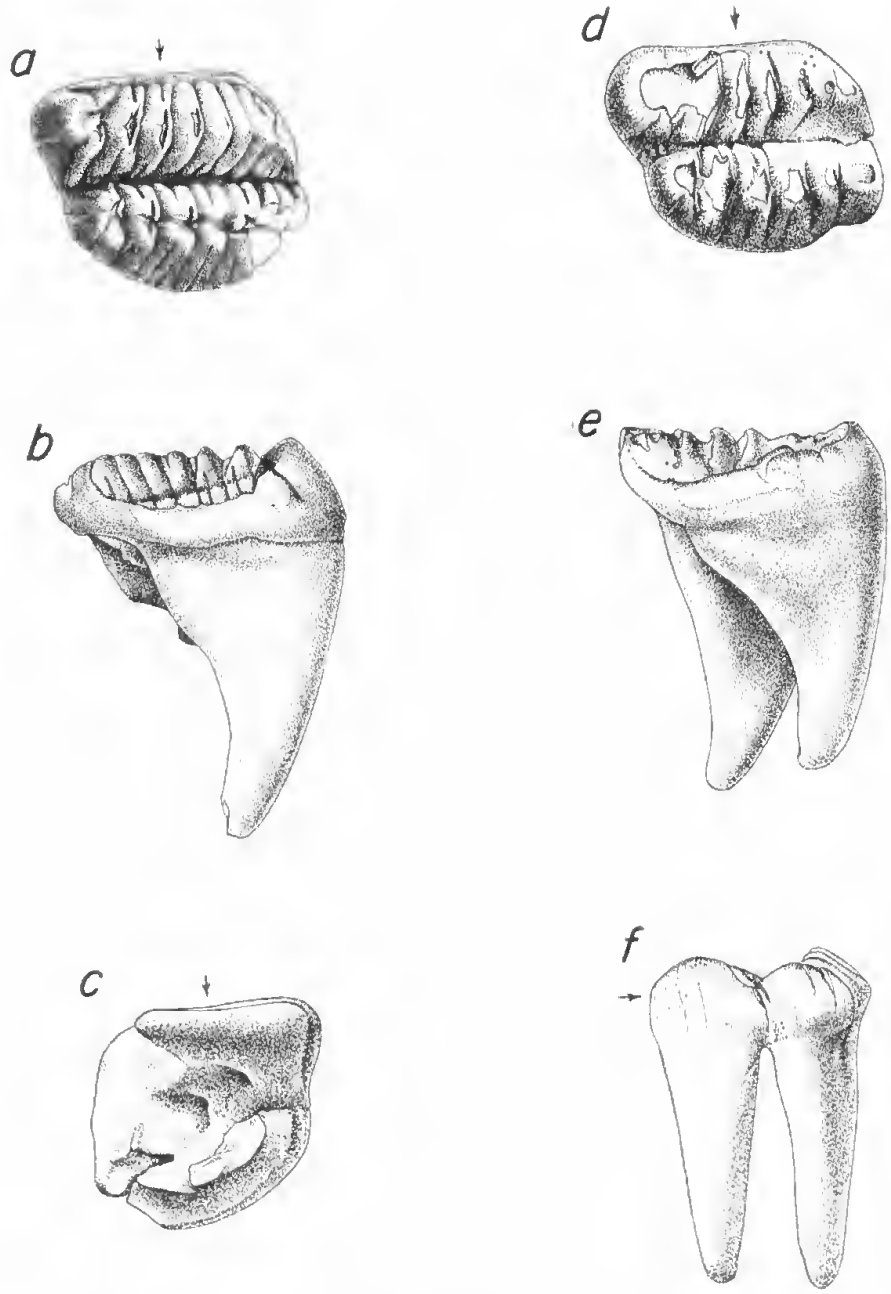

FIG. 7

Ektopodon serratus, n. gen. et. sp. Paratypes. *a* occlusal, *b* anterior, *c* ventral view of UCMP 67173, left lower molar; *d* occlusal, *e* anterior, *f* labial view of UCMP 67174, left lower molar. Four times natural size. Note appression facette at anterior base of crown. Arrow indicates anterior surface of tooth.

[6] ἔκτοπος—odd, strange; and ὀδούς—tooth.

Generic diagnosis: Mammals with triangular upper and subquadrate lower teeth of lophodont construction. Lophs (ids) divided into numerous ensps (ids). Basic construction of upper and lower teeth nearly identical. Largest cusp of upper teeth on lingual side of each loph, largest cuspid of lower teeth on labial side of each lophid. Lophs (ids) strongly separated by narrow, deep, transverse valley. Labial and lingual occlusal outline constricted at transverse valley. Roots of lower molars restricted to primary (labial) side of lophids. Upper molars with a labial and lingual pair of roots with a possible additional root under the anterior loph. Lingual pair of roots tend to be fused into a single structure.

Ektopodon serratus[7] Stirton, Tedford and Woodburne, n. sp.

Holotype: South Australian Museum, P13847; left upper molar.

Paratypes: UCMP 67173, unworn left lower molar; UCMP 67174, moderately worn left lower molar; UCMP 67176, well worn right lower molar.

Specific diagnosis: That of genus until other species are described.

Type locality: UCMP Loc. V6213, 1,835 feet north of V5858, east shore of Lake Ngapakaldi, South Australia.

Horizon: Wipajiri Formation; pebble conglomerate, unit 3 of measured section 5 (Appendix).

Age: Kutjamarpu fauna, middle Tertiary; probably Miocene.

Description—Upper molar: The tooth has been oriented as though it were a left upper molar (fig. 6) for reasons which will be developed below. Whether or not this orientation ultimately proves to be correct, it at least serves to facilitate the present description. The length of the tooth, as measured perpendicular to the flat posterior surface is 7.2. The greatest transverse width (8.2) was measured perpendicular to the length. The tips of all roots were either abraded away or broken off.

The occlusal surface of the tooth is widely triangular in outline, with the apex of the triangle directed anteriorly (fig. 6a). A flat, strap-shaped surface is present on the posterior side (fig. 6e). This is interpreted as an appression facette caused by wear against an adjacent tooth in the dental series. A small flattened surface on the anterolabial side of the anterior loph suggests that another tooth was present in the maxillary anterior to SAM P13847. The small size and oblique orientation of the facette indicates that the posterior end of the tooth which caused it would have had a different shape from that

[7] *serratus*—serrate, in reference to the nature of the transverse lophs.

of SAM P13847, and may have been a premolar. Irrespective of which tooth SAM P13847 actually represents, the enamel-covered crown consists of three parallel transverse lophs. The crown is supported by a labial and lingual pair of roots whose basic construction parallels that of the middle and posterior lophs.

The transverse width of the anterior loph is 3.5. It has four crescentically arranged cusps with the second from the lingual side being the largest. The lingual-most cusp slopes laterally against the second cusp. These two cusps are separated laterally and across the crest of the loph by a wide groove; posteriorly the groove is much narrower. The two labial cusps are smaller and more closely appressed. Their features are largely obscured by abrasion of their anterior surfaces.

The second loph is 13.0 wide and is composed of nine cusps. The posterior loph is 13.6 wide and has eight cusps. The largest cusp on each loph is found at the lingual tip of the loph. In occlusal view, the lingual surface of each lingual cusp is strongly convex. The cusps of the middle and posterior lophs are elongate anteroposteriorly, have a blunt, rounded apex, and slant labially from base to tip. The cusps diminish in size labially along each loph to such an extent that the last two are difficult to separate. The anterior and posterior sides of the cusps slope toward the base of the loph at an angle of about 45°, then plunge vertically into the deep, but narrow, transverse groove which separates each loph. The anterior and posterior surfaces of the cusps in the first two lophs slope at about the same angle. In the posterior loph, the posterior side of the cusps is steeper than the anterior. A groove which slants laterally toward the apex is cut into the anterior and posterior sides of most of the cusps. These grooves separate an anterior and posterior pair of root-like ridges on the basal part of each cusp. The grooves terminate just above the bottom of the transverse valley. The anterior faces of the three small cusps at the labial end of the middle loph are united into a smooth surface which is directed anterolingually. The last two labial cusps of the posterior loph also lack grooves, but the commissure between the cusps is still visible. A flat, elongate, strap-shaped facette is developed on the posterior surface of the last loph (fig. 6e). This is similar to facettes on the anterior surface of the lower teeth (fig. 7b, 7d) and is interpreted as an appression facette caused by wear between adjacent teeth.

SAM P13847 has a pair of labial and lingual roots (fig. 6d). The lingual pair slant lingually away from the tooth and are joined throughout their length by an anteroposterior septum. The root-mass thus

formed tapers distally and is reminiscent of the single internal root commonly found in the upper teeth of mammals. The labial root under each loph (fig. 6h) diverges from its lingual counterpart. The anterior labial root is oriented anterolingually toward the anterior tip of the tooth, but also sends off a thin transverse septum toward the base of the anterior lingual root. Most of the root below the anterior loph is broken away. The configuration of the remaining portion suggests that the anterior loph was supported by a single root whose base was connected to the labial root under the middle loph. The posterior labial root is oriented transversely and is composed of a labial and lingual portion. These two parts are mainly swellings in the basic root-mass and are broadly connected by a slightly thinner transverse segment of bone. The root structure thus formed underlies the labial two-thirds of the base of the posterior loph.

Lower molars: The lower molariform teeth are basically like the type specimen with the exception that they have only two transverse lophs and are thus trapezoidal in outline. Except for the short anterior loph of the upper molar, the nearly identical configuration of the upper and lower teeth is striking. UCMP 67173 and UCMP 67174 are illustrated in fig. 7. These two teeth are considered to be left last lower molars because of the appression facettes of their anterior sides and because the greatest development of the roots occurs on the labial side of the teeth. The largest cuspid in each lophid also occurs on the labial side.

The anteroposterior length of the teeth was measured perpendicular to the flat anterior face. The greatest transverse width was measured perpendicular to the length. The height of the roots was taken as the distance perpendicular to a line drawn through the base of the enamel. The measurements for the various lower teeth are as follows: UCMP 67173: anterior length is 5.8, width is 7.2; height of anterior root is 8.0. UCMP 67174: length is 5.8, width is 7.0; height of anterior root is 7.3; posterior root is 7.8. UCMP 67176: length and width of this tooth are approximate because of its extreme stage of wear and a slight amount of displacement along a crack developed in the transverse valley. Length is 5.8, width is 8.0; height of anterior root is 7.4, posterior root is 7.5.

In each tooth there are eight cuspids in the anterior lophid and six or seven in the posterior. UCMP 67176, a right last lower molar, is too worn for an accurate count of its cuspids to be made. Enough of the dental pattern remains, however, to indicate that this tooth had a similar configuration to the others. All of the lower teeth described

seem to come from the same position in the jaw. That UCMP 67176 is from the opposite side of the jaw has already been pointed out.

In UCMP 67173, the grooves on the posterior face of the cuspids on the last lophid extend farther toward the apices than in the upper molar. On the anterior lophid of the lower molars, these grooves are much less developed than in the upper. The anterior and posterior sides of the cuspids slope toward the base at an angle of about 45°. Although UCMP 67174 is in a later stage of wear, the configuration of the cuspids and grooves seem to agree with that in UCMP 67173. Both of these teeth show heaviest wear on the side which we have oriented as labial. This is also the side of the tooth on which the heaviest development of the roots occurs.

In labial view, the main axes of the two roots are essentially parallel, although they curve slightly anteriorly (fig. 7f). In anterior view (fig. 7b, e) it can be seen that the tip of the anterior root is almost directly under the labial edge of the tooth whereas the greater lingual curvature of the posterior root causes its tip to lie in a more medial position. There seems to be no significant difference in the sizes of the two roots.

The basic plan of the lower teeth is a pair of transverse lophids which have been subdivided by a number of cuspids. The orientation of the roots which support the lophids is also transverse (fig. 7e). Like the upper tooth, the lower molars of *Ektopodon* are transversely lophodont, although the coalesced lingual pair of roots in the upper molars may indicate that such lophodonty developed from a basically triangular tooth.

Affinities: The structure of the teeth of *Ektopodon* is not paralleled in any rodent known to us. The geologic and paleozoogeographic setting of the Australian continent indicates, therefore, that the ancestors of this unusual animal should be sought among the Monotremata, Marsupialia, primitive Placentalia, or even earlier groups. Based on the present study and those of Butler (1939), Green (1937), Patterson (1956) and Simpson (1928, 1929a and b) the configuration of the molars and roots of various therian and non-therian groups may be summarized as follows:—

Triteylodontidae: Teeth not tribosphenic; cusps arranged in longitudinal rows; more rows in upper teeth; upper and lower teeth basically similar; either four or five roots in upper teeth, two in lowers; lower roots lie directly under the crown of the tooth; posterior lower root larger than anterior.

Tricenodonta: Teeth not tribosphenic; cusps arranged in longitudinal rows; upper and lower teeth basically similar; only two equal roots in either upper or lower teeth; lower roots lie directly under the crown of the tooth.

Multituberculata: Teeth not tribosphenic; cusps arranged in longitudinal rows, more rows in upper teeth; upper and lower teeth of basically similar construction; upper and lower teeth with two roots; lower roots lie directly under the tooth crown; lower roots variable, generally equal in size.

Symmetrodonta: Upper teeth triangular, lower teeth slightly so; cusps arranged in triangular fashion; upper and lower teeth relatively similar; two, possibly three, roots in upper teeth, two in lowers; lower roots lie directly under the tooth crown; posterior root large in upper and lower teeth.

Ektopodon: Teeth not tribosphenic; cusps arranged in transverse lophs; construction of upper and lower molar crown nearly identical; upper molar with three (?four) roots, lowers with two; lower roots developed primarily on labial side of tooth; lower roots essentially same size.

Ornithorhynchus: Teeth degenerate; generally an anterior and posterior moiety separated by a transverse valley, upper teeth with prominent lingual cusp from which one or two ridges pass transversely to the labial side, lower teeth with prominent labial cuspid in each moiety which tends to be elongated into a transverse crest; upper and lower teeth basically similar; embryological studies suggest that each moiety is supported by a transverse root.

Docodonta: Upper teeth transversely rectangular; lowers longitudinally rectangular; cusps basically in longitudinal rows with secondary transverse orientation; three roots in upper teeth, two in lowers; upper and lower teeth different; lower roots lie directly under the crown; lower roots equal sized.

Pantotheria: Teeth tribosphenic; cusps arranged in triangular fashion; upper and lower teeth different; three roots in upper, two in lower teeth; lower roots lie directly under the crown; posterior lower root smaller than anterior.

Metatheria and Eutheria: Teeth tribosphenic; cusps arranged in triangular fashion; upper and lower teeth different; three roots in upper, two in lower teeth; lower roots lie directly under the crown; lower roots generally equal in size.

Tritylodontids, triconodonts and multituberculates possess dentitions with low-crowned non-tribosphenic teeth in which the cusps are arranged in longitudinal rows. The upper and lower teeth of these forms are of basically similar construction. The fact that tritylodontids have been classed as reptiles (Romer, 1956) emphasizes the general similarity of the dentition of animals near the reptile-mammal transition. Although appearing later in time than the others, the multituberculates retained this primitive type of dentition. The two-rooted condition of the upper and lower molars found in the triconodonts persisted into the symmetrodonts, although there is a possibility that the latter tended to develop three-rooted upper teeth in the Cretaceous (Patterson, 1956, p. 11).

The symmetrodonts, contemporaneous with the tritylodontids and triconodonts, departed from the basic dental pattern by developing teeth in which the cusps had a triangular orientation. Their upper and lower molars were, however, still basically similar.

At first glance, the docodont dentition seems to represent a rather radical departure from the primitive mammalian type. A strongly transverse, rather than longitudinal, orientation is given to the teeth by the development of transverse crests in the molars, one in the uppers, two in the lowers. Upon closer inspection (see Simpson,

1929a, pls. XVIII-XX) it is apparent, however, that docodont molars consist basically of two longitudinal rows of cusps with secondary cross-crests. The cross-crests descend from each side toward a median longitudinal valley; lophodonty is at best incipient. It is also apparent that the basic construction of the upper and lower molars is similar. The addition of a median longitudinal emargination in the anterior and posterior end of the docodont lower molar would produce a configuration essentially like that of the upper. The development of three roots in the upper molars is a possible advance over the condition in triconodonts and symmetrodonts, and the incipient transverse lophodonty is unique among Mesozoic mammals.

The Pantotheria, Metatheria and Eutheria seem to be too advanced to be considered for the ancestry of *Ektopodon*. The Mesozoic and early Cainozoic members of these groups clearly have tribosphenic molars which do not even remotely resemble those of *Ektopodon*. It is true that some marsupials and placentals have developed transversely lophodont dentitions, but not ones in which the upper teeth are as similar in detail to the lowers or in which the anterior loph is so nearly identical to the posterior.

The most reasonable statement that can be made concerning the ancestors of *Ektopodon* is that they are not presently known. The general degree of advancement shown by its dentition suggests that *Ektopodon* represents a pre-therian lineage. Although no reptile has been known to develop teeth like these, the possibility of basal relationships with the mammal-like reptiles cannot be definitely excluded on present evidence. The development of three-rooted upper molars and the incipient transverse lophodonty found in the Docodonta form a basis for interesting speculations, but the long interval of time involved dictates that these remain mere speculations.

Ancestry of the Monotremata: The origin and phyletic position of these animals, so clearly mammalian in some respects and so obviously reptilian in others, has long been a taxonomic problem. *Tachyglossus* is unfortunately excluded from this discussion by its lack of dentition. The transient molars of *Ornithorhynchus* have been most recently discussed by Simpson (1929b) and Green (1937). From figures and descriptions in these two works it is clear that *Ornithorhynchus* teeth consist of an anterior and posterior moiety separated by a transverse valley. In the upper teeth there is a labial and lingual constriction at the transverse valley. Simpson (1929b) has provided a detailed description of the *Ornithorhynchus* cheek teeth.

Simpson (*ibid.*, p. 7) considered that the teeth were basically composed of two transverse halves, each with a primary lingual upper and lower labial cusp, and that the numerous accessory cusps had no particular significance other than indicating the degenerate nature of the teeth. After reviewing various possibilities Simpson (*ibid.*, p. 14) concluded that the teeth of *Ornithorhynchus* were probably not derivable from any known mammalian type, that the only even remotely possible exception to this might be the triconodonts. A similar conclusion was reached by Green (1937, p. 404) except that he favours the Haramiyidae (Microcleptidae) as a possible ancestor. It is interesting to note that a sufficient number of longitudinal and transverse elements are present in docodont molars to form the structural basis for the teeth of both *Ektopodon* and *Ornithorhynchus*.

Ektopodon and *Ornithorhynchus* both have a simple lophodont dentition in which the largest cusp is located on the lingual side of each upper loph, the labial side of each lower lophid. Embryological studies suggest that if any orientation of the roots in *Ornithorhynchus* can be said to be preferred, it is transverse (Green, 1937, fig. 14). There is also a random proliferation of secondary roots due to the degenerate nature of the teeth. The condition of the lower roots in *Ektopodon*, in which the fang is restricted to the labial or primary side of the tooth, may be attributed to the possibility that the dentition of this animal was becoming degenerate. The nearly random proliferation of cuspules in the teeth of *Ornithorhynchus* may indicate that the teeth had degenerated from a dentition in which cuspules were present, but in a more regulated configuration. Such a configuration could have resembled the transverse proliferation of cuspules seen in *Ektopodon*.

In summary, the molariform teeth of both *Ektopodon* and *Ornithorhynchus* have a simple, bilophate structure which is not closely approached in any other group of mammals. The teeth of *Ektopodon* represent a structural pattern from which the degenerate dentition of *Ornithorhynchus* could be derived. In view of the rather limited data now available it is possible that *Ektopodon* and *Ornithorhynchus* are members of separate, collateral, lineages and are not related orthogenetically. If *Ektopodon* is a monotreme it is the first Tertiary record of the order and points to the long expected but unrecorded diversity of the group. The level of structural development of the dentition in *Ektopodon* and *Ornithorhynchus* is reminiscent of that found in the Docodonta and suggests that the Monotremata originated from non-therian rather than therian mammals.

Subclass THERIA
Infraclass Metatheria

Order **Marsupialia**
Phascolarctidae

Litokoala[8] Stirton, Tedford and Woodburne, n. gen.
(Fig. 8)

Genotypic species: *Litokoala kutjamarpensis* n. sp.

Generic diagnosis: M^1: smaller and labial outline more convex than in *Phascolarctos*, length and width 5.7; space between metacone and hypocone greater than between paracone and protocone; small anterolingual and posterolingual crests ascending from apices of

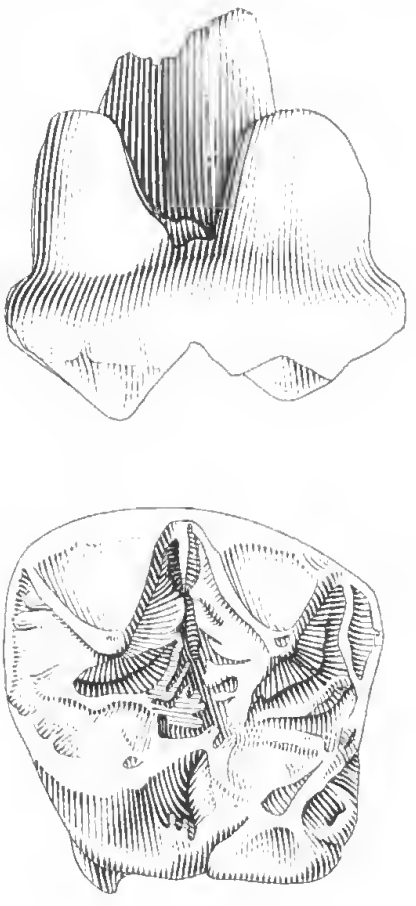

FIG. 8

Labial and occlusal view of RM^1 of *Litokoala kutjamarpensis*, SAM P13845, Kutjamarpu fauna. Approximately two-thirds natural size.

[8] λιτος and *Koala*, to emphasize the relatively simple occlusal pattern of the holotype in comparison with *Perikoala* and *Phascolarctos*.

paracone and metacone; labial cingulum not extended across base of metacone; posterior spur of protoconule directed posterolingually toward transverse valley where it fades out in posterior part of wide longitudinal valley between paracone and metacone; low crest continuous from anterolabial corner of protoconule along anterior base of paracone to labial cingulum; crescentic metaconule present; enamel surfaces moderately crenulate between anterior spurs of metaconule, and on posterior base of paracone; elsewhere in longitudinal and transverse valleys enamel surface smooth.

Litokoala kutjamarpensis[9] Stirton, Tedford and Woodburne, n. sp.

Holotype: South Australian Museum, P13845; right upper first molar in early stage of wear. We have identified this tooth as M^1 on the basis of the following features which are similar to that tooth in *Phascolarctos*. Crescentic anterior cingulum; anterior cingulum continuous with protoloph lingually, widely separating paracone from anterior edge of tooth; metacone slightly higher than paracone, and hypocone higher than protocone; cingulum continuous across labial base of metacone; crescentic stylar structure at anterior base of protocone which forms small pocket in that area.

Specific diagnosis: That of genus until other species are described.

Type locality: UCMP Loc. V6213, 1,835 feet N. 1° E. of V5858, east shore of Lake Ngapakaldi, South Australia.

Formation: Wipajiri Formation: pebble conglomerate, unit 3 of measured section 5 (Appendix).

Age: Kutjamarpu fauna, middle Tertiary; probably Miocene.

Description: The Kutjamarpu tooth is smaller than in *Phascolarctos*; its greatest length and width is 5.7. The four principal cusps are prominent and pyramidal in outline. Although the protocone is more worn it seems clearly to have been lower than the hypocone[10]. The relative heights of these cusps also prevail in M^1 of *Phascolarctos*; however in the living koala the cusps are equal in height or nearly so on M^2, but the reverse is true on M^3 and M^4 where the paracone and protocone are higher than the metacone and hypocone. In the Kutjamarpu M^1 the distance between the metacone and hypocone is greater than between the paracone and protocone; the reverse is true

[9] In reference to the occurrence of the species in the Kutjamarpu fauna.

[10] Hypocone is used here only in a topographic connotation. Homology with cusps in a similar position on upper molars of some placental mammals is not implied. In another genus from the Kutjamarpu fauna the evidence seems clear that the cusp in question is developed from the posterior wing of the protocone, rather than from a cingulum or as a twinning of the protocone as has occurred in most placental mammals.

throughout the tooth row in *Phascolarctos*, and probably *Perikoala*. The triangular labial surfaces of the paracone and metacone in P13845 slope gently to the apices of the cusps.

Other distinctive characters in the Kutjamarpu M^1 indicating phascolarctid affinities are seen in the anterolingual and posterolingual crests ascending from the apices of the paracone and the metacone. In *Phascolarctos* only the posterolingual crest of the paracone is present. These crests do not occur in *Schoinobates* or *Pseudocheirus*.

The pattern of attrition on the molars is apparently the same in both *Litokoala* and *Phascolarctos* in that the anterior and posterior edges of the paraselene and metaselene contribute equally to the shearing function of the tooth. In *Pseudocheirus* and *Schoinobates* most of the shearing is done by the posterior crests of those selenes.

The labial outline of the Kutjamarpu tooth, in direct occlusal view, is somewhat more convex than in M^1 of *Phascolarctos*. The sloping labial surface opposite the paracone is narrower and more concave anteroposteriorly than the surface opposite the metacone. Furthermore the base of the paraconal surface is crossed by a cingulum, whereas that of the metacone is unobstructed. *Phascolarctos* differs in having a cingulum across the base of each of these surfaces in M^1. In *Pseudocheirus* and *Schoinobates* the cingulum on the paraconal surface is incomplete because a groove passes from the middle of the surface to the base of the tooth. The metaconal surface of those genera also differs in that a crest ascends posterodorsally from mesostyle II so that the surface is unobstructed only at its posterolabial corner.

The stylar cusps in *Litokoala* are not as prominent as in *Phascolarctos* and can be seen best by their triangular outline from the labial side. The parastyle, as in *Phascolarctos*, is far back from the anterolabial corner of the tooth and is connected to the paracone by the anterior wing of the paraselene. In M^1 of both *Pseudocheirus* and *Schoinobates* the parastyle is at the extreme anterolabial corner of the tooth and is separated from the base of the paracone by a deep cleft.

In *Litokoala*, the stylar cusps decrease slightly but progressively from the parastyle to the metastyle, whereas in *Phascolarctos* the height of the styles on M^1 in descending order are mesostyle II, mesostyle I, parastyle and metastyle.

The protoconule is separated from the protoloph in *Litokoala* and occurs at the anterolingual base of the paracone. The posterior spur of the protoconule is directed posterolingually toward the transverse valley where it fades out in the posterior part of the wide

longitudinal valley between the paracone and metacone. In *Schoinobates* and *Pseudocheirus* the spur is relatively longer, crescentic, and is connected to the posterolingual base of the paracone. *Phascolarctos* also differs from the Kutjamarpu tooth in having a short crescentic spur that connects to the anterolingual base of the paracone. A low crest is continuous from the anterolabial corner of the protoconule along the anterior base of the paracone to the labial cingulum. This structure is not seen in the koalas we have for comparison. In M^1 of *Pseudocheirus* the protoconule is connected directly to the parastyle, whereas in *Schoinobates* it first joins the anterior cingular extension of the protoloph which continues on to the parastyle. The surface of the protoconule in the Kutjamarpu tooth is smooth whereas in *Phascolarctos* ridgelets and grooves between them give a rather boldly crenulate effect to the conule. A low but distinct ridgelet extends posteriorly from the protoloph in the lingual side of the longitudinal valley.

A structure identified by us as a modified metaconule occurs as a very low crescentic crest medial to the lingual base of the metacone. Its posterior spur extends back into the valley between the metacone and the hypocone but is closer to the metacone. This structure is not present in *Phascolarctos* or in the M^2 of *Perikoala*. Anteriorly the metaconule in the Kutjamarpu specimen divides into two spurs. One extends anterolabially into the transverse valley between the metacone and paracone, but does not reach as far labially as in *Schoinobates* or *Pseudocheirus*. The other spur is directed anterolingually and is separated from the junction of the metaloph crest of the protocone and the anterolabial crest of the hypocone by a narrow groove. In *Litokoala* there is a short transverse ridgelet connecting the metaconule with the anterolabial crest of the hypocone. The enamel surface between the anterior spurs of the metaconule, on the labial surface of the junction and on the posterior basal surface of the paracone, is crenulate; but elsewhere in the longitudinal valley between the main cusps, the enamel surface is smooth. This is in marked contrast to *Phascolarctos* and *Perikoala* in which the longitudinal valley is deeply crenulate.

The protocone and the hypocone are much more widely rounded in the Kutjamarpu tooth than in *Perikoala* and *Phascolarctos*, consequently the anterior and posterior wings of those selenes do not stand out as sharply in relief in *Litokoala*. Another phascolarctid character is the connection of the metaloph crest of the protocone and the anterolabial crest of the hypocone. This closes the transverse valley area lingually well in from the inner edge of the tooth. In

Schoinobates and *Pseudocheirus* the posterior of these crests bypasses the anterolabial crest of the hypocone. A rather bulbous cusplike structure occurs at the anterolingual base of the hypocone. It connects across to the base of the protocone forming a pocket between it and the crest formed by the junction of the metaloph crest of the protocone and the anterolabial crest of the hypocone. The cusplike structure is subdued in *Phascolarctos*, and its connection across to the protocone is more cingulumlike, is longer and fades out at the lingual base of the protocone. These features are even more subdued in *Pseudocheirus* and *Schoinobates*. Both *Litokoala* and *Phascolarctos* have a short stylar structure at the anterolingual base of the protocone. It, however, is more crescentic and forms a deeper pocket in the fossil. In

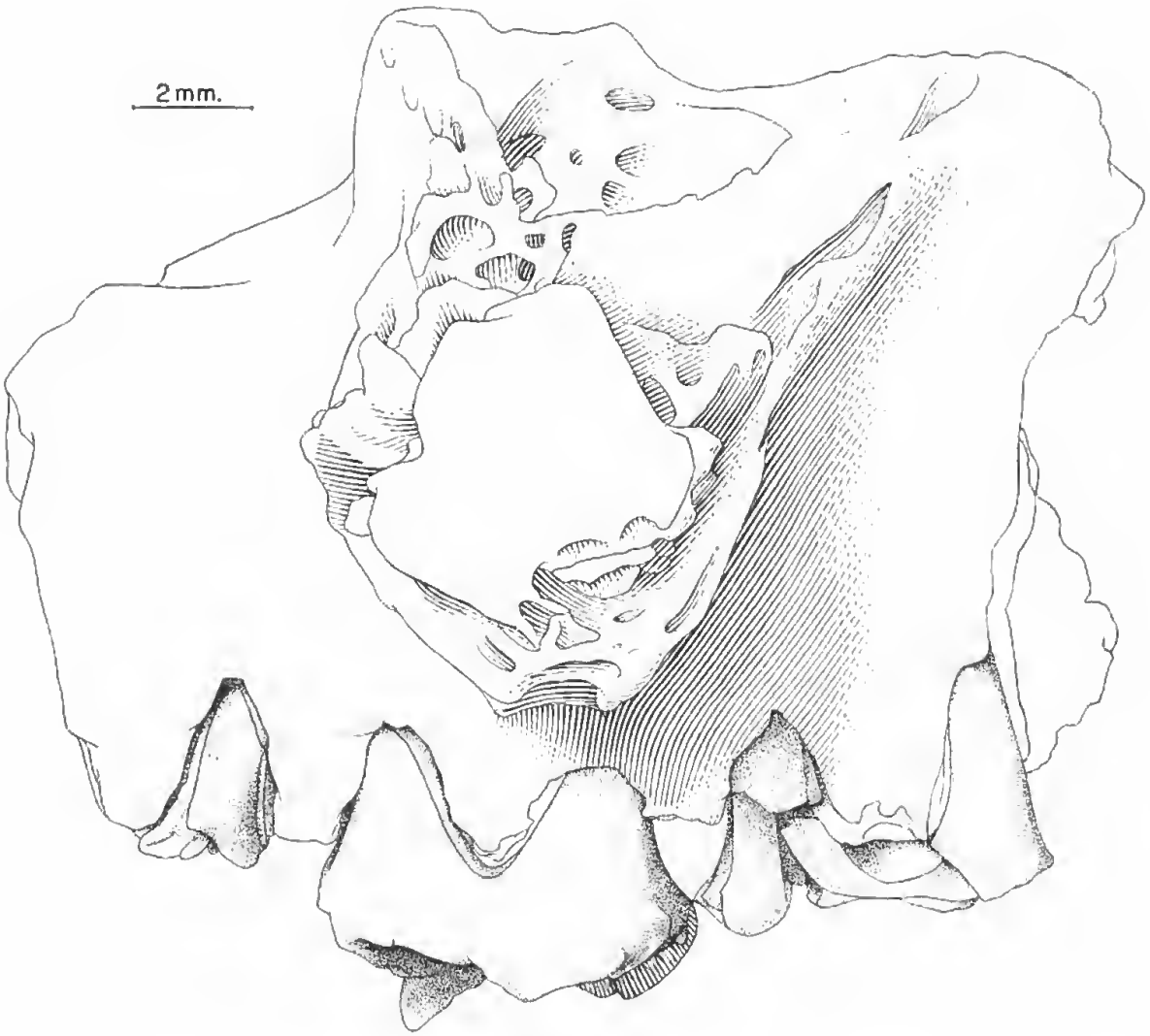

FIG. 9

Labial view of right maxillary fragment of *Perikoala palankarinnica*, UCMP 45343. Approximately two-thirds natural size.

Phascolarctos this feature diminishes progressively from M^1 to M^4. It is not present in *Pseudocheirus* or *Schoinobates*, and is apparently absent in *Perikoala*.

Paratype of Perikoala palankarinnica: The paratype of *Perikoala palankarinnica* from the Etadunna Formation is a right maxillary fragment (UCMP 45343) with a partial alveolus of P^3, roots of M^1, M^2 with the crown partly preserved and an alveolus of M^3 (figs. 9, 10).

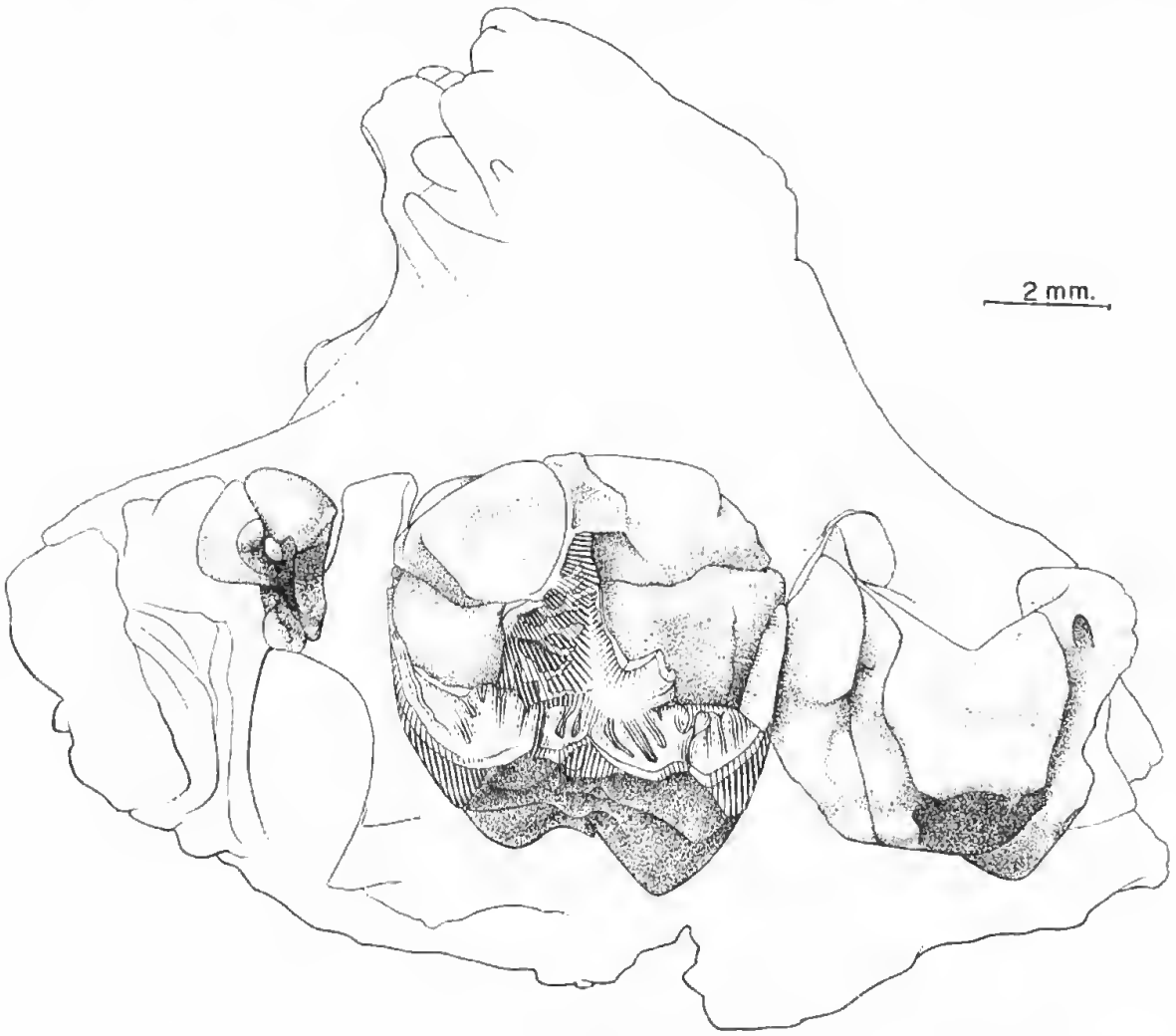

FIG. 10

Occlusal view of right maxillary fragment of *Perikoala palankarinnica*, UCMP 45343. Approximately two-thirds natural size.

Nearly all of the body of M^2 is present, only the lingual cap is absent from the paracone and the posterolingual face of the metacone. The unobstructed labial surface of the metacone and the absence of the metaconule agree with the M^2 of *Phascolarctos*. Although most of the lingual base of the paracone is missing, there is no suggestion on the remaining portion that an anterolingual stylar cusp was present.

This suggests further agreement with M^2 of *Phascolarctos* as compared with M^1. The length and width of the tooth are both approximately 5.9.

The tooth is essentially unworn as far as can be seen, which may to some extent account for the profusely crenulate nature of the crown enamel. The enamel appears to have been smooth on the lingual surfaces of the hypocone and protocone, and is smooth on the labial surface of the metacone; but on the labial surfaces of the protocone and hypocone and the anterior surface of the metacone and adjacent areas, the enamel is strongly crenulated. The distribution and intensity of crenulation equals that of comparably worn specimens of the koala and is thus different to the condition in *Litokoala*.

In *Litokoala* and in *Phascolarctos*, a ridgelet extends posteriorly from the protoloph in the lingual side of the longitudinal valley. In *Perikoala*, the *function* of a raised structure in this area of the tooth is maintained by a series of transverse ridgelets directed labially from the protocone and protoloph. Each of these ridgelets terminates abruptly at the axis of the longitudinal valley in a small, raised conule. A line connecting the apices of these terminal conules passes posteriorly from the protoloph in a similar orientation and position as does the protoconule ridgelet in the Kutjamarpu tooth and in *Phascolarctos*. In RM^1 and LM^3 and LM^1 of two specimens of *P. cinereus* at hand, the configuration seen in *Perikoala* is present; whereas in the other molars of those two specimens, as well as all the molars of two other Recent specimens, a ridgelet is present. This suggests that the condition in *Perikoala* is a variation upon a functional plan, and may also indicate that the *function* is as important as the *means* by which it is achieved. The lack of this ridgelet in *Perikoala* in contrast to the condition in the other animals does not necessarily remove *Perikoala* from the direct ancestry of *Phascolarctos*.

The labial border of the tooth as seen in occlusal view is oblique anterolabially, which suggests that the transverse diameter across the anterior half of the tooth was greater than that across the posterior half. This agrees with the condition in M^2 of *Phascolarctos* and differs from *Litokoala* in which the transverse diameter across the respective parts of the tooth is essentially the same. This may be due to the fact that the Kutjamarpu tooth is M^1. M^1 in *Phascolarctos* is more nearly equidimensional transversely across the anterior and posterior halves than M^2.

In *Perikoala* and *Phascolarctos*, a metaconule is not present as a distinct cusp, the enamel being highly crenulate in that area. On the other hand, the presence of a distinct metaconule in *Litokoala* is in

direct contrast to this and it may represent a primitive feature which has been retained from an earlier level of organization.

The metaloph in *Perikoala* curves smoothly from the protocone posterolabially to meet the anterolabial crest of the hypocone. This is more typical of M^2 than M^1 of *Phascolarctos* in which the posterior arm is directed posterolabially and then turns abruptly labially before joining the arm from the metaconule.

Except for its smaller size those parts of the tooth which can be compared in *Perikoala* agree with M^2 of *Phascolarctos*. The only significant similarity to *Litokoala* is size but the more complex enamel crenulations and the absence of the metaconule tend to preclude close affinity between *Perikoala* and the Kutjamarpu form, although both may have had some pre-Ngapakaldi common ancestor.

In ventral view, the anterior root of the zygoma in *Perikoala* lies directly above M^2, its anterior surface slopes smoothly on to the maxillary above M^1 and its posterior face is concave posteriorly. In lateral view, the labial edge of the anterior face is directed anterodorsally, not vertically as in *Phascolarctos*. The root of the zygoma is essentially symmetrical in lateral view in that the anterior and posterior surfaces slope equally toward each other and meet ventrally so that a sagittal section through the root would be triangular, with the apex ventral. In *Phascolarctos*, the anterior surface is vertical while the posterior surface slopes anteroventrally. Thus, a sagittal section through the root would be asymmetrical with the apex of the triangle shifted anteriorly. *Phascolarctos* possesses a ventral boss at this apex which is oriented anterolingually in ventral view, is thickest medially and tapers laterally and posterodorsally along the lateral surface of the arch. The zygoma in *Phascolarctos* occupies the maxillary from above the midpoint of M^1 to the rear of M^2, its anterior face possesses a strong antorbital fossa below the infraorbital foramen.

As compared to that of *Phascolarctos*, the anterior root of the zygomatic arch in *Perikoala* is smaller both longitudinally and transversely, has no ventral boss, is more symmetrical in the sagittal plane, apparently lacks a concave antorbital fossa below the infraorbital foramen, and the anterior face slopes anterodorsally in lateral view rather than being vertical. All of these characters point to the more primitive nature of *Perikoala*, and may be related functionally to the *masseter* being less well developed in *Perikoala* as compared with *Phascolarctos*.

Remarks: As discussed by Stirton (1957), the lower dentition of *Perikoala* is more primitive than *Phascolarctos*, and a similar statement can be made concerning the fragmentary upper tooth described

above. It seems clear, however, that *Perikoala* and *Phascolarctos* are more closely allied than either is to *Litokoala*. The latter apparently represents a persistently primitive side branch which diverged, at some point in the early Tertiary, from the lineage leading toward *Phascolarctos*. On the other hand the basic similarity of *Phascolarctos*, *Perikoala* and the Kutjamarpu form shows that these animals represent a major phyletic branch, possibly within the Phalangeroidea excluding *Pseudocheirus* and *Schoinobates*. At the present time, the most reasonable taxonomic assignment of the latter two genera seems to be with the Phalangeridae.

TABLE OF MEASUREMENTS

	Phascolarctos cinereus				*Litokoala*	*Perikoala*
	UCMP 71665	UCMP 58801	UCMP 58800	UCMP 22814	SAM P13845	UCMP 45343
Lengths						
RM¹	8.1	7.5	7.9	7.8	5.7	
LM¹	8.3	7.4	7.8	7.9		
RM²	7.8	7.8	8.0	7.6		5.9*
LM²	7.8	7.8	7.9	7.9		
Widths						
RM¹	8.2	7.8	7.7	7.8	5.7	
LM¹	8.1	7.8	7.7	7.8		
RM²	8.4	7.9	7.9	7.7		5.9*
LM²	8.2	7.8	8.0	7.9		

* Approximate.

Vombatidae

Rhizophascolonus[11] Stirton, Tedford and Woodburne, n. gen.

(Fig. 11)

Genotypic species: *Rhizophascolonus crowcrofti* Stirton, Tedford and Woodburne, n. sp.

Generic diagnosis: P^3: bilobed; anterior lobe round, enamel on lingual and labial sides; posterior lobe 3.8 wider transversely than long anteroposteriorly; enamel on rounded lingual side, absent on labial side; from edge of enamel posteriorly occlusal outline curves obliquely anterolabially then around into labial inflection; shallow opposing lingual and labial inflections; height of enamel about 16.1 above root on lingual side, on anterolabial side 4.3; one small labial and two well developed lingual roots.

Rhizophascolonus crowcrofti[12] Stirton, Tedford and Woodburne, n. sp.

Holotype: South Australian Museum P13846, moderately worn left P^3.

11 ῥίζο φάσκολος—in reference to the rooted character of the holotype in comparison with teeth of *Phascolomus*.

12 In honour of Dr. W. P. Crowcroft, Director of the South Australian Museum.

Specific diagnosis: That of genus until other species are described.

Type locality: UCMP Loc. V6213, 1,835 feet north of V5858, east shore of Lake Ngapakaldi, South Australia.

Horizon: Wipajiri Formation; pebble conglomerate, unit 3 of measured section 5 (Appendix).

Age: Kutjamarpu fauna, middle Tertiary; probably Miocene.

Description: This family is represented by a left upper P^3 that is clearly referable to a new genus. It differs markedly from the living and Pleistocene wombats in having one small labial and two well developed lingual roots, and in the height of the crown.

The crown is bilobed as emphasized by shallow labial and lingual inflections. The anterior lobe is essentially round; its transverse width is 7.5. The transverse dimension of the posterior lobe is 10.6, whereas anteroposteriorly it measures 6.8. Although the inner half of the posterior lobe is uniformly rounded, from near the posterior midline the outline curves obliquely anterolabially then around into the labial inflection. This part of the occlusal outline is accentuated by the absence of enamel on the side of the tooth in that area. Otherwise a 1.0 layer of enamel starting at the labial inflection extends around the anterior lobe into the lingual inflection where it is very thin, then continues around the lingual side of the posterior lobe to terminate on the posterior surface.

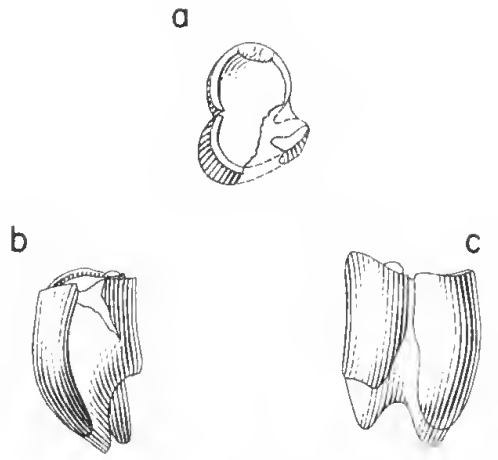

FIG. 11

Rhizophascolonus crowcrofti, n. gen. et. sp. *a* occlusal view, *b* posterior view, *c* lingual view of holotype, LP^3. SAM P13846. Natural size.

One of the most interesting features is a small, liplike, remnant of enamel that folds back from the anterior edge over a small part of the otherwise extensive exposure of dentine. The remaining enamel is slightly grooved at the midline with higher points on each side.

This bit of enamel therefore is suggestive of an enamel covering of the occlusal surface at and near this level. If so, the height of crown of the tooth in a young animal was little if any higher than in the tooth at hand.

The tooth is curved labially and has the greatest exposure of enamel on the lingual surface. Below the anterior root on the lingual side the enamel measures 11.8, and below the posterior root it is 16.1, whereas on the labial side of the anterior lobe the enamel height is 4.3.

The lingual inflection widens from about 0.8 at the edge of the occlusal surface to 4.0 at the base of the enamel. This inflection is largely filled with cement which coalesces with the dentine of the roots dorsally. The roots are partly abraded but their tapering outlines indicate that the longest one was not more than 7.0 in length.

Remarks: The distribution of the enamel and dentine in the occlusal pattern, the labial curvature and the apparent incipient hypsodonty of its P^3 indicate that *Rhizophascolonus* is a wombat.

The bilobed outline and the size of the premolar seems to reveal that *Rhizophascolonus* is more closely related to *Phascolonus* than to *Ramsayia, Lasiorhinus* or *Vombatus*. The lobes of P^3 in *Phascolonus* are of different shape than in *Rhizophascolonus*; there is no enamel on the labial side of the anterior lobe, and the tooth is extremely hypsodont and rootless. *Ramsayia* and *Lasiorhinus* differ from the other wombats in having P^3 with a triangular occlusal outline and in lacking either a labial or lingual inflection, but as in *Phascolonus*, enamel is absent on the labial side of the anterior lobe. In *Vombatus* the occlusal outline is nearly triangular but there is an anterolingual groove and the enamel encircles the tooth.

If *Rhizophascolonus* is ancestral to *Phascolonus*, the rate of evolution in hypsodonty is much like that which occurred in the development of the Pleistocene beaver *Castoroides* from *Monosaulax*, which lived during the Miocene, even though the increase in tooth size in the beaver lineage is much greater than in the wombats.

Evidence from the P^3 of *Rhizophascolonus* seems to indicate that the *Phascolonus* lineage extended well back into the Miocene if our correlations are reasonably correct. Therefore, the common ancestor for all of the known genera of wombats may have lived well back in the Oligocene.

A

B

FIG. 12

A. View from lake of UCMP loc. V-6213, type locality of Kutjamarpu fauna and Wipajiri Formation. Quarry is at edge of lake; tractor is standing on dune deposits.

B. Closer view of Wipajiri Formation at V-6213 showing coarse dark basal clastic deposits overlain by lighter, thinly bedded leaf-bearing shales. Dip of beds indicate channel configuration. Shovel is approximately horizontal. White 6in. ruler shows scale.

ENVIRONMENT

As indicated in the faunal list the Kutjamarpu is one of the most diverse Tertiary vertebrate faunas yet uncovered in Australia. The large number of forest dwelling types indicates that the stream in which the Wipajiri Formation was deposited passed through a wooded area. This is consistent with the setting implied by the abundant impressions of *Eucalyptus* leaves found in the upper portion of the formation. The riparian situation represented by the Wipajiri Formation and its contained fossils indicates the former presence of climates which were more hospitable than those which now obtain in this part of Australia.

AGE OF THE KUTJAMARPU FAUNA

The peramelids, phascolarctids and macropodids have their closest affinities with forms in the Ngapakaldi fauna. The wombat is more primitive than any known Pleistocene or Recent member of the family. The ancestral position of *Neohelos tirarensis* to *Kolopsis torus* from the late Miocene Alcoota fauna of the Northern Territory (Stirton, Woodburne, and Plane, 1967), strongly points to a Miocene age for the Kutjamarpu fauna. On the present evidence, the best estimate of the age of the Kutjamarpu fauna is post-Ngapakaldi and pre-Alcoota, probably closer to that of the Ngapakaldi fauna. The Wipajiri Formation was thus deposited after the Etadunna Formation and before the Mampuwordu Sands. The Wipajiri is the second oldest formation in the five-fold stratigraphic succession of Tertiary rocks in the Tirari Desert and, as compared with the age assignments given to the other faunas in the area, is probably Miocene in age.

APPENDIX A

Measured Section 1

At UCMP Locality V5858, North-east shore, Lake Ngapakaldi; type locality of Ngapakaldi fauna. (See fig. 2.)

Unit	Description	Thickness
1	*Gypsiferous drift sand*, orange red	18in.
UNCONFORMITY		
ETADUNNA FORMATION		
2	*Claystone*, dark grey; arenaceous particles sparsely distributed throughout. "Greasy" appearance on freshly broken surface. Basal intraformational breccia.	3in.
3	*Claystone*, dolomitic, light grey. "Greasy" texture on fresh surface. Basal intraformation conglomerate of green claystone fragments.	15in.
4	*Claystone*, grey green to green with scattered fine grained quartz sand and silt. Fossil mammals at top (UCMP Locality V5858), *Ngapakaldi fauna*. Base not exposed.	15in. +
		51in. +

Measured Section 2

1,165′ N. 8° W. of V5858 (see fig. 2)

Unit	Description	Thickness
1	*Gypsiferous drift sand*; orange red	3in. +
UNCONFORMITY		
ETADUNNA FORMATION		
2	*Claystone*, dark grey; arenaceous particles sparsely distributed throughout. Freshly broken surface has "greasy" appearance.	13in.
3	*Claystone*, light grey, slight greenish tinge; lacks "greasy" appearance on fresh surface.	4in.
4	*Claystone*, dark grey, as unit 2, but possibly slightly higher fraction of arenaceous particles. "Greasy" appearance on fresh surface. Basal intraformational breccia 6in. thick consisting of a lighter grey claystone matrix enclosing angular to subrounded particles of light calcareous mudstone (unit 5) and a dark grey claystone. Thin (¼in.) layer of gypsum variably separating units 4 and 5.	30in.
5	*Claystone*, calcareous (dolomitic), light grey. "Greasy" texture on fresh surface. Scattered occasional particles of both lighter mudstone and dark brownish grey claystone. Basal contact with underlying green claystone (fossiliferous at V5858) indicated by intraformational conglomerate of rounded to subrounded particles of pebble and coarse sand sized fragments of the green claystone. Total depth not reached.	12in. +
		62in. +

Measured Section 3

In 24ft. long pit (Pit 1) trending N. 4° E., whose N. end is 49′ S. 68° E. from centre of main quarry (V6213) of *Kutjamarpu fauna*. See fig. 4.

Unit	Description	Thickness
1	*Dune sand*	30in.
UNCONFORMITY		
WIPAJIRI FORMATION		
2	*Shale*, dark grey, thinly laminated, with scattered gypsum crystals. Leaf remains. 5ft. to north the bed thickens to 30in. Lenses of well sorted angular white sand grains are interbedded in lower part in association with turtle remains. (Corresponds with unit 2, section 5.)	9in.
3	*Claystone*, dark green, with ferruginous partings; scattered gypsum fragments, clay pebbles and rounded duricrust fragments occur throughout. Larger claystone pebbles found near base (probably corresponds to unit 3, section 5).	12in.
4	*Claystone*, light green, highly limonitic	1in.
5	*Pebble conglomerate*, green claystone, light calcareous mudstone and light grey claystone clasts of Etadunna formation in light grey claystone matrix. Local centres of limonite stain and gypsum crystals interspersed. Selenite near base. Main fossil concentration; numerous remains of fish, turtle, crocodile and occasional mammals (probably corresponds to part of unit 3, section 5).	5in.

UNCONFORMITY		
ETADUNNA FORMATION		
6	*Claystone to siltstone*, light grey; "greasy" when wet (probably corresponds to unit 2, section 4).	2 to 6in.
7	*Claystone*, limonite stained	1in.
8	*Claystone*, calcareous, dark grey. Base not reached. (Probably corresponds to unit 3, section 4.)	6in. +
		66in. +

Measured Section 4

North end of pit 2, 14′ S. 29° W. of centre of V6213. See fig. 4

Unit	Description	Thickness
WIPAJIRI FORMATION		
1	*Sandstone*, brown, ferruginous, with green claystone and limonitic pebbles; gypsum partings. Thickens to north-east (corresponds to unit 3, section 5).	2in.
UNCONFORMITY		
ETADUNNA FORMATION		
2	*Claystone*, light grey, with scattered fine sand-sized arenaceous particles. This apparently combines units 2 and 3 of section 2.	24in.
3	*Claystone*, dark grey, with basal intraformational breccia consisting of angular to subrounded fragments of light calcareous mudstone and darker brown claystone in matrix dark grey claystone.	20in.
4	*Claystone*, light grey, calcareous (dolomitic); green intraformational breccia at base.	24in.
5	*Claystone*, green. Same as fossiliferous unit at V585. Base not exposed.	4in.
		74in.

Measured Section 5

Along line a-b (fig. 4) in main quarry of *Kutjamarpu fauna* (V6213) 1,835ft. N. 1° E. of type locality of *Ngapakaldi fauna* (V5858). See fig. 4 and fig. 12, A.

Unit	Description	Thickness
1	*Dune sand*	6in.
UNCONFORMITY		
WIPAJIRI FORMATION		
2	*Shale*, dark grey, finely laminated, containing plant remains. Limonitic stain at base. Occasional arenaceous partings with limonite stain, and lenses of fine sand with green clay balls or arenaceous green clay associated with turtle remains.	31in.
3	*Pebble conglomerate*, rounded green, occasionally blue, claystone clasts, with scattered ferruginous sandstone clasts (smaller size than in unit 5), rounded duricrust fragments, irregular siliceous clasts. Upper 2in. ferruginized. Main vertebrate fossil horizon of *Kutjamarpu fauna*.	7in.

4	*Claystone*, blue, with scattered large green claystone clasts and limonite concretions and pebble-sized green and brown claystone clasts. Contains impressions of unionid pelecypods and vertebrate remains.	3in.
5	*Conglomerate*, pebble to boulder sized clasts, mainly rounded green sandstone, claystone and subrounded red ferruginous sandstone fragments in a limonite coated sand matrix. More angular light to dark grey claystone clasts derived from underlying Etadunna formation. Scattered rounded duricrust clasts and angular fragments of chert. Conspicuous large turtle fragments usually standing on edge. Contains fish, reptile and mammal remains.	4in.
UNCONFORMITY		
ETADUNNA FORMATION		
6	*Claystone*, light grey, base not reached	
		51in.

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Dr. R. A. Stirton died suddenly on June 14th, 1966 while this paper was in press. This great loss is keenly felt for "Stirt" was a person of rare ability, enthusiasm and generosity and an inspiration to all who knew him. The inquiry into the history of the Australian mammals had been one of his major interests for over a decade and it is largely through his stimulus that much of the present knowledge concerning the Tertiary vertebrates of that continent has been brought to light. Our association with Dr. Stirton on these and other studies has been a thoroughly enjoyable and rewarding experience and it is our intention to carry on, as far as possible under the circumstances, the Australian projects he initiated.

R. H. Tedford and M. O. Woodburne.